

AUSTRAL HEPATICAE, VIII. TUYAMAELLOIDEAE

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The Lejeuneaceae subfamily Tuyamaelloideae Schust. & Kachroo was established in Schuster (1963, pp. 82, 91) for genera "intermediate in some respects between the Nipponolejeuneoideae. . . and the Paradoxae." In Schuster (1963a, 1968) the genera Siphonolejeunea Herz., Tuyamaella Hatt., and Austrolejeunea (Schust.) Schust. are referred here; a revised key is given in Schuster (1968) and a further refinement of this appears in Grolle (1973), which includes the new, distinctive, monotypic genus Nephelelejeunea Grolle.

Grolle (l.c.) removed Siphonolejeunea nudipes from that genus, where both Herzog (1948) and I (Schuster, 1963) had placed it and transferred it to Austrolejeunea; he regarded A. olgae (Schust.) as an "extreme f. depauperata" of S. nudipes. In this contribution I shall refute both of these positions and present a diagnosis of a new species of Austrolejeunea, A. hispida.

I. The Distinction of Austrolejeunea and Siphonolejeunea

Austrolejeunea first appears in Schuster (1963, p. 187) as a subg. of Siphonolejeunea, founded for S. olgae Schust. The subgenus (and species) were stated to differ from other taxa assigned to Siphonolejeunea, including, of course, the Australasian S. nudipes in "the non-tubular lobules with 3 sharp, conspicuous teeth; the entally displaced hyaline papilla; the stem with only 3 medullary cell rows; the filiform underleaf lobes." In Kachroo & Schuster (1961) it is shown that the hyaline papilla in Siphonolejeunea s. str. is basically marginal and, on mature lobules, is inserted between two cells, lying side-by-side, forming a very low and blunt vestige of an apical tooth. Only on leaves with reduced lobules -- a feature very common in both S. nudipes and S. neesii (S. nudicalycina Herz.) -- do we find, in common with many other Lejeuneaceae where reduced lobules may occur, a sharper apical tooth with the hyaline papilla terminal thereon. This feature alone suffices to definitively separate the three known species of Austrolejeunea from the three known species of Siphonolejeunea. In fact, Grolle (l.c., p. 252) in his key to genera of Tuyamaelloideae also adopts this as a generic criterion and remarks that in Austrolejeunea the hyaline papilla is "deutlich ental" while in Siphonolejeunea it is stated to be marginal or "kaum ental." In view of the fact that in A. olgae the "hyaline papilla [is] entally displaced and inserted on or at [the] base" of the apical tooth (Schuster, 1968, p. 512; author's original emphasis), it seems incomprehensible that A. olgae was placed as a synonym of S. nudipes.

Furthermore, it is clear from Grolle's own figures (fig. 2:a-c)

that the hyaline papilla in S. nudipes, on leaves with mature and inflated lobules, always arises from the faint notch between two bulging cells, situated side-by-side, jointly forming the faint apical tooth of the lobule. The student is invited to compare the condition in fig. 2:a-c in Grolle with fig. 15:12, 15 (of S. nudicalycina) in Kachroo & Schuster (1961). It is clear that both taxa are immediately similar in the (a) obscure apical tooth formed not by a single projecting cell but by two not or hardly projecting cells situated side-by-side; (b) position of the marginal hyaline papilla in the sinus between these cells; (c) strong variation in lobule development, the weaker lobules often having an apical tooth with a terminal hyaline papilla (as in fig. 15:13-14, in Kachroo & Schust., l.c.). On the basis of the key characters in Grolle (l. c., p. 252) "Lobulus oft + reduziert. . . am apikalen Rand ein undeutliches Zähnchen mit marginaler oder kaum entaler Hyalinpapille. . . ." Siphonolejeunea nudipes keys to Siphonolejeunea, while A. olgae, on the basis of the key characters ("Lobulus stets voll ausgebildet. . . am freien Rand [mit] 2-4 Zähne, von denen der am weitesten distale deutlich ental die Hyalinpapille trägt. . . .") keys clearly to Austrolejeunea in his key.

Other key characters, cited in both Grolle (1973) and Schuster (1963, 1968), exhibit more ambivalence. It was the ambiguity of these features, at several levels, that initially led me to regard Austrolejeunea as a mere subgenus of Siphonolejeunea. (1) in S. nudipes, the lobule is often + reduced, but in the advanced S. schiffneri, lobules are typically uniformly tubularly inflated and well developed. Grolle states that in Austrolejeunea, where he would place S. nudipes, the lobule is "stets voll ausgebildet" when, in actuality, S. nudipes shows excessive variation in lobule development. This criterion is thus ambiguous, although in the three species I here assign to Austrolejeunea the lobule is always inflated and well developed (see, e.g., pl. 64:1,6,7 in Schuster, 1968). (2) In Siphonolejeunea the stem medulla has "+ 5 cell rows" (Schuster, 1968, p. 511) while in Austrolejeunea it has "3 cell rows." In S. nudipes only 3 cell rows occur, although Kachroo & Schuster (1961, fig. 15:8) show 5 cell rows in the medulla of S. nudicalycina. (3) Austrolejeunea almost invariably bears paired innovations, as originally noted in Schuster (1963, p. 83) whereas Siphonolejeunea has single subfloral innovations (Kachroo & Schuster, l.c., figs. 15:1, 16:1; Schuster, 1963, p. 83). However, S. nudipes has mostly single innovations although (at least in RMS 51635, Little Barrier I., N.Z.) occasional gynoecia bear paired innovations. (4) Discoid gemmae are abundant in Siphonolejeunea (both S. nudicalycina and S. schiffneri; see fig. 16:7 in Kachroo & Schuster, l. c.) and may occur in extraordinary abundance in S. nudipes (in, e.g., RMS 51635 they are not only in the "usual" position occupied in Siphonolejeunea, the adaxial, or postical, lobe surface, but also to a lesser extent on some antical lobe surfaces and, exceptionally, even perianth surfaces). By contrast, I have studied numerous individuals of all three species of Austrolejeunea and have seen only rare traces of gemma production -- usually not even the gibbous initials on the lobe surface can be found. This

is true of both corticolous and epiphyllous populations.

Two facts emerge from this discussion: (1) In some respects, *S. nudipes* -- which I regard as a "synthetic," primitive species -- occupies a middle ground between *Siphonolejeunea* and *Austrolejeunea*. This fact -- and especially prolonged study (in 1962, of the material of RMS 51635, collected March 11, 1962; again in 1974) of abundant material of *S. nudipes* -- has convinced me that one could, with excellent reason, consider *Austrolejeunea* as a mere subgenus of *Siphonolejeunea*. In other respects, *S. nudipes* is sharply distinct from all known taxa of both *Austrolejeunea* and *Siphonolejeunea*: it has, e.g., a long-stipitate perianth, while the remaining taxa all have nonstipitate perianths (compare Kachroo & Schuster, l.c., figs. 15-16; Schuster, 1968, pl. 64). In this respect *S. nudipes* closely approaches *Nephelolejeunea* (compare figs. 1:a and 2:n in Grolle, 1973). Indeed, if we were to merge *Austrolejeunea* and *Siphonolejeunea*, it would then be necessary to also reduce *Nephelolejeunea* to a mere subgenus. It seems more rational to retain the three genera and recognize the simple fact that with the sole species, *S. nudipes*, we have a "Bindungsglied" or synthetic species. (2) Using the criteria cited below, one can equally argue that the two groups should be retained, at least as subgenera.

Key to Genera

1. Lobules (often reduced, exc. in the advanced *S. schiffneri*) with hyaline papilla never entally displaced: on mature lobules situated in the faint notch between two weakly or hardly projecting cells constituting, technically, the obscure apical tooth; on reduced lobules, terminal on a 1-celled apical tooth. Gemmae nearly always abundant. Underleaves with lobes merely acute or even blunt, at base 3-4 cells broad, 2(3) cells broad to within 1(2) cells of apex. Gynoecia normally with 1 subfloral innovation (if, occasionally, with 2, in *S. nudipes*, the perianth is longly stipitate). Larger plants, with leaves 1.4-2 mm wide or more.

Siphonolejeunea Herz.

1. Lobules (except rarely at branch bases) always inflated and rather uniformly developed, with a sharply distinct 1-celled apical tooth at or near whose ental base the hyaline papilla is inserted. Gemmae nearly constantly lacking. Underleaves with lobes filiform, formed of (3)4-6 or more cells in a single row, at base only 2-3 cells broad. Gynoecia nearly always with paired innovations; perianth never stipitate. Small plants, with leaves 525-875 μ wide.

Austrolejeunea (Schust.) Schust.

II. AUSTROLEJEUNEA (Schust.) Schust.

As I have redefined the genus Austrolejeunea, above, S. nudipes must stay in Siphonolejeunea. In the latter, there is a marked tendency, linked with copious gemma production, for large leaf cells (see infra); in Austrolejeunea leaf cells are much smaller and plants, as a whole, are smaller.

These distinctions, and those of the three species of Austrolejeunea, emerge from the following key.

Key to Species

1. Leaves + uniform and lobulate throughout: each lobule large, 0.45-0.75 area of lobe; hyaline papilla inserted, entally, on inner face of a 1-celled apical tooth. Perianths not or short-stipitate. Mature shoots with underleaf lobes ending in 3-4 moniliform single cells or more. Gemmae rare. Subfloral innovations, at least usually, paired, elongating. 2.
2. Lobular teeth strongly unequal: the largest (median) formed of 2-3 superposed cells, inserted on 2 cells side-by-side. Heteroecious: gynoecia always (or usually) with antheridia in bracts or subfloral bracts, but with accessory separate androecia. Underleaf lobes ending in 4-6 single cells. [New Zealand]. 3.
3. Cells of keel and lobe surfaces, and of perianth keels and surfaces convex but never produced as conoidal, thick-walled papillae. A. olgae (Schust.) Schust.
3. Cells of keel and of lobe surfaces, of perianth keels and (to a lesser extent) intervening surfaces strikingly armed with conoidal, somewhat thick-walled elevations, the leaves subhispid. A. hispida Schust., sp. n.
2. Lobular teeth subequal, the largest usually formed of a single cell inserted on 2 basal cells lying side-by-side. Autoecious. Cells of leaf surfaces, keel, and perianths not conoidally armed. [Fuegia-S. Chile] A. radulaefolia (Massal.) Schust.
1. Leaves strikingly polymorphic: many to most with lobules reduced to a basal, linear fold lacking teeth; larger lobules under 0.45 lobe area; hyaline papilla marginally inserted between 2 cells forming the apical tooth. Perianth becoming long-stipitate. Mature shoots with underleaf lobes 2-4 cells wide at base, ending in 1-2 single cells. Gemmae abundant. Subfloral innovations normally single. S. nudipes (H. f. & T.) Herz.

1. Austrolejeunea olgae (Schust.) Schust.

Described in detail in Schuster (1968, pp. 512-13; pl. 64). In that diagnosis several relevant points are emphasized: (a) lobules with apical tooth formed of a single cell, with hyaline papilla entirely displaced on this cell; (b) median lobular tooth 2-3-celled, sometimes from a 2-cell-wide base; (c) underleaf lobes filiform and 2-3 cells wide only at base, the lobes uniseriate for a length of (3)4-6 cells; (d) gynoecia with 2 widely divergent innovations; (e) lobules large, constantly well developed; (f) perianth merely "emergent" at maturity, but not long-stipitate; (g) plants 770-876 μ wide with leaves; (h) cells firm, with very distinct trigones, small: marginal 16-20, median 17-22 x 16-24 μ .

Grolle (1973), without studying material of this taxon, placed it as a synonym of S. nudipes ("Austrolejeunea nudipes"), regarding it as an "extreme f. depauperata," and expressing astonishment that I had not noted the "engen Beziehungen" between these two taxa. There are no such close similarities between these two taxa, however, and S. nudipes differs from A. olgae in all eight criteria emphasized above, showing in contrast: (a) mature lobules with apical "tooth" a rounded-marginate protuberance, with hyaline papilla inserted between these two cells; (b) the largest lobular tooth -- often not at all elaborated -- formed at most of 1 or 2 superposed teeth; (c) underleaf lobes typically lingulate or tapered-lingulate, 3-4(5) cells wide at base, the apices ending in 1 or at most 2 single cells; (d) gynoecia nearly constantly with a single subfloral innovation; (e) lobules very variable, often vestigial or reduced to a lingulate lamella, often without marginal teeth distinct -- or the apical tooth, alone, elaborated, often even that vestigial; (f) perianth at maturity strikingly stipitate; (g) plants relatively vigorous, sterile axes 1400-1750 μ wide with leaves; (h) cells leptodermous, much larger; marginal (19)21-25 μ , median from 24-30 x 25-32 to 26-34 x 30-36 μ , the marginal swollen, lobes thus conspicuously crenulate. These distinctions prove, beyond any doubt, that A. olgae is not immediately allied to S. nudipes.

In criteria a-h A. olgae is clearly immediately allied to the new species A. hispida Schust. It differs principally, but not absolutely, in the smooth leaf cells. Nowhere -- on keel, lobe margins or surfaces, or keels and surfaces of the perianth -- does one find a trace of conoidal cell elevation. In this respect A. olgae closely approaches the South American A. radulaefolia. The distinction of these two taxa is clear from the above key.

2. Austrolejeunea hispida Schust., sp. n.

Species A. olgae similis, differens, autem, ut cellulae foliorum sinusulatim tuberculatum.

Plants light yellow-green, epiphyllous or corticolous on small twigs (of Pseudowintera), creeping, Cololejeunea-like, leaves not

closely appressed (in situ, diagnostically somewhat elevated above axis and substrate), irregularly but copiously branched; branches, except for the paired Radula-type innovations all gyrothecal, Lejeunea type, widely patent. Shoots to 770-810 μ wide; stems (48) 50-62 μ in diam., with 7 cortical + 3 medullary cell rows, the cells all firm-walled. Leaves remote to subcontiguous, clearly elevated above substrate, obliquely to widely patent, moderately convex; lobe narrowly obovate, ca. 550 μ long x 375 μ wide (smaller on branches), rounded at apex, the margins faintly crenulate (locally denticulate when cellular tubercles are marginally oriented), strongly narrowed towards base. Lobule strongly inflated, ca. 0.5-0.55 lobe length (310-325 μ long x 165-180 μ wide), widest distally, the inflated sector fusiform-elliptical, but entire apical region plane, appressed to lobe, tridentate; lobular teeth consisting of a distal-most tooth, situated about midway in the oblique sinus between the keel and the large middle tooth, 1-celled, the cell usually inflated and large; middle tooth large, sometimes curved, usually straight, usually of 3 cells in a row, arising from 2 cells lying side-by-side; proximal tooth formed of a single blunt cell inserted usually on 3 cells, side-by-side; hyaline papilla ental. Underleaves oblong to narrowly ovate-lingulate, bifid ca. 0.7-0.8, from ca. 70 x 150 to 75-90 x 155-182 μ , the sinus very narrowly U-shaped to almost slit-like, the erect lobes 2(3) cells wide at base, mostly formed of uniseriate, + moniliform cells; disk short, with conspicuous rhizoid-initial disk, at times appearing almost stalked; rhizoid-initial disks conspicuous, especially on older sectors of leading shoots. Cells rather thin-walled, with + distinct, usually concave-sided trigones; each lobe cell, and cells in distal 0.5-0.65 of keel, elevated as a firm, conspicuous, rather high, + thick-walled tubercle; cuticle otherwise smooth. Marginal cells slightly smaller than inner cells, 12-15(16) μ ; median cells of free lobe ca. 15-18(20) x 15-21(22-25) μ . Asexual reproduction not seen.

Heteroecious [sometimes paroecious, but often with accessory, separate, androecial branches]. Androecia often on + elongated branches [sometimes originating as subfloral innovations], with 2-4 pairs of bracts; bracts leaflike but lobules larger, more inflated, with the apical teeth reduced or vestigial; diandrous; bracteoles present throughout. Gynoecia terminal on branches of the Lejeunea type, of varying length, always with paired innovations; innovations widely spreading, often at nearly right angles to fertile axis. ϕ Bracts narrow, 0.5-0.75 length of mature perianths, highly polymorphous: basically with a lingulate to lingulate-obcuneate lobe, ca. 550-625 μ long x 185-230 μ broad, rounded to bluntly angulate at apex, entire-margined but feebly crenulate through the agency of weakly protuberant cells and, here and there, marginally projecting "tubercles"; lobules linear-lingulate, ca. 400-455 μ long x 115-125 μ wide, free for only the distal 0.2-0.35, the free apex typically 2-3-dentate. Bracteole free, ca. 90-100 μ wide, 250-265 μ long, ca. 0.65-0.75 bifid, with erect, usually closely juxtaposed, linear-subulate lobes only 2-3 cells wide at base, uniseriate for 4-6 cells distally, the cells moniliform. Perianth obovoid, inflated, in

distal 0.35 clearly 5-plicate, ca. 650 μ long x 360 μ in distal diam., shortly rostrate; keels, and locally the intervening surface, roughened with conoidally elevated tubercles, much as on leaves. After fertilization, perianth occasionally rather stipitate and emergent beyond bracts.

Sporophyte very small; capsule ca. 275 μ in diam.; seta ca. 155 μ in diam. (with 12 epidermal + 4 inner cell rows), formed of only ca. 8-9 cell tiers; foot rudimentary, few-celled. Epidermal capsule-wall cells in 1-2 marginal rows, firm-walled, oblong, ca. 13-15 x 21-25 μ ; interior cells larger, polyhedral, irregular, 22-25 x 35-42 to 28-30 x 45 μ , thinner-walled except at angles, where rounded. Inner cell layer of delicate cells, rectangulate on margins, irregularly polyhedral within margins, narrow and elongated in central-basal areas, thin-walled, at angles and along longer walls with hyaline, nodular thickenings [surface view]. Elaters ca. 14 (3 + 4 + 3 + 4), ca. 16-18 x 180-210 μ , colorless, with a nodular-thickened wall [profile]. Spores large, 22-25 x (30)36-48(56) μ to 22-23 x 75-80 μ , with well-spaced, sharply defined, small papillae and, in scattered loci, stellate groups of cuneiform papillae.

Type. New Zealand, South Island: Falls Creek, Upper Hollyford R. valley, along Milford Rd., Fiordland Natl. Park (RMS 48809; Nov. 3, 1961). The type was collected on leaves and twigs of Pseudowintera colorata, in part mixed with Metzgeria, Frullania, and Cololejeunea spp.

In the distinct, conoidally elevated leaf cells (of the lobes, keelar region, perianth keels, and, to some extent, intervening perianth surfaces), this species recalls various taxa of Cololejeunea and Colura. In other respects, A. hispida is exceedingly close to A. olgae and I have hesitated for more than 15 years before becoming convinced that it deserves species status. I have again compared the respective types; aside from the leaf cells, they are indeed exceedingly similar. The similarity extends to the gynoeical bracts which tend to have the free apex (2)3(5)-dentate and irregular in A. hispida -- exactly as shown in pl. 64:6 in Schuster (1968), for A. olgae. In this respect the bracts, which average equal to the leaves in size, are much more leaflike in form. By contrast, the bracts, which in S. nudipes show gross variation from gynoeicum to gynoeicum, always appear to have narrow, linguulate lobules that are blunt to rounded-truncate at the apex and edentate -- as in the other two species assigned to Siphonolejeunea.

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